A NEW DICYNODONT (REPTILIA, THERAPSIDA) FROM *CYNOGNATHUS* ZONE DEPOSITS OF SOUTH AFRICA[1]

By

Nicholas Hotton III

Smithsonian Institution, Washington, D.C. 20560

(With 2 plates, 1 figure and 1 table)

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Introduction

A small dicynodont skull, complete with lower jaw and stapes, was collected by J. W. Kitching about 1,6 km south of Lady Frere, Cape Province, on the north side of the Cacadu River in 1961, during the writer's first visit to South Africa. It was originally catalogued as number 22936 in the collections of the National Museum of Natural History, Smithsonian Institution, but as it must be designated the type of a new genus, it has been transferred to the collections of the Bernard Price Institute for Palaeontological Research, Johannesburg, where it is catalogued as Museum Number 430.

The specimen is clearly a member of the *Cynognathus* zone fauna, for it was found in the same shale layer as a good skull of the *Cynognathus* zone gomphodont *Diademodon*, about 275 m west of the latter. No. 430 lay right side up, about 0,3 m below a layer of fine gray sandstone that was about 0,6 m thick. Although the skull is markedly distorted by dorsoventral flattening, preservation of the bone is good and I do not think it possible that the specimen was reworked from older deposits. The area is part of Lady Frere Commonage, which has yielded numerous specimens characteristic of the *Cynognathus* zone but nothing to suggest the presence of any other therapsid faunal element, either by survival or by reworking of older sediments.

The specimen is definitely not a member of the genus *Kannemeyeria*, which until now was the only dicynodont present in the *Cynognathus* zone fauna. It is also distinguishable from other dicynodont genera, and so constitutes a second, very rare, dicynodont member of the *Cynognathus* fauna.

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Taxonomy

Class **REPTILIA**

Order THERAPSIDA

Family **Dicynodontidae**

Genus ***Kombuisia***[2] gen. nov.

Kombuisia frerensis[3] sp. nov.

Genoholotype. No. 430. Skull with articulated stapes and lower jaw, strongly distorted by dorsoventral flattening, but very little cracked or broken; zygomae lost. Sub-periosteal bone very well preserved; little evidence of surface cracks due to subaerial weathering.

Generic diagnosis. Small dicynodont (see Table I for dimensions) without post-canine teeth, much like *Kingoria* (Cox 1959) in the following features. Interorbital bar wider than intertemporal bar, and length of postorbital region nearly equal to distance from postorbital bar to snout (Plate 1 A). Nasal boss expressed only as a low, rugose median swelling on frontals, nasals, and premaxilla; no postfrontal bone; preparietal fusiform, long and narrow; postorbitals cover only about three-quarters of medial sides of temporal fenestrae; parietals exposed dorsally as narrow ridge between postorbitals. Caniniform processes small, rounded. Secondary palate very long, choanae well behind back of caniniform processes (Plate 2 A). Secondary palate consists almost entirely of premaxilla, which is in contact with small palatal process of palatine bone and blocks maxilla from contact with choanal margin (Plate 2 A). Palatine makes very minor contribution to secondary palate; ectopterygoid separates maxilla from pterygoid. Insertion of temporal musculature on lateral face of dentary produced laterally to form prominent shelf or 'wing' (cf. Cox 1959).

Table 1

Measurements of *Kombuisia frerensis*, No. 430, TYPE, in millimetres. Greatest height and height at snout omitted because of crushing.

Overall length, occipital condyle to tip of premaxillary beak (L)	76,8
Width at postorbital bar (W)	52,3
Smallest interorbital distance (Wio)	16,1
Intertemporal width, anterior end of intertemporal bar (Wit)	12,7
Width across paroccipital processes (Wo)	32,2
Bottom of occipital condyle to top of occipital plate, direct (Ho)	18,6
Horizontal distance, anterior margin of orbit to tip of premaxillary beak (Rao)	15,9
Horizontal distance, posterior margin of orbit to tip of premaxillary beak (Rpo)	35,1
Length of temporal fossa, medial side (Rt)	27,5
Length of intertemporal bar, postorbital bar to top of occiput (Rit)	26,0
Posterior width of mouth, measured between posteromedial margins of caniniform processes at level of anterior maxillary margin (P_1)	20,0
Length of mouth, along midline from P_1 to tip of premaxillary beak (P_2)	23,0

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[2] The genus is named for its discoverer, J. W. Kitching, who during his military service bore the nickname 'Kombuis', Afrikaans for kitchen.

[3] The specific name refers to the type locality of *Kombuisia*.

Dentary symphysis long. External naris large, distance from front of orbit about twice diameter of external naris, which lies very close indeed to margin of upper jaw.

Differs from *Kingoria*, and from other dicynodonts as well, in configuration of dentary. Symphysis shallow, broad, flat dorsally; ventral profile slopes upward and forward very gently from splenial margin to tip of beak, so that general appearance of front of beak is spatulate (Plate 2 C). Front and side margins of beak sharp. In dorsal aspect (Plate 2 B) the symphysis is not parallel-

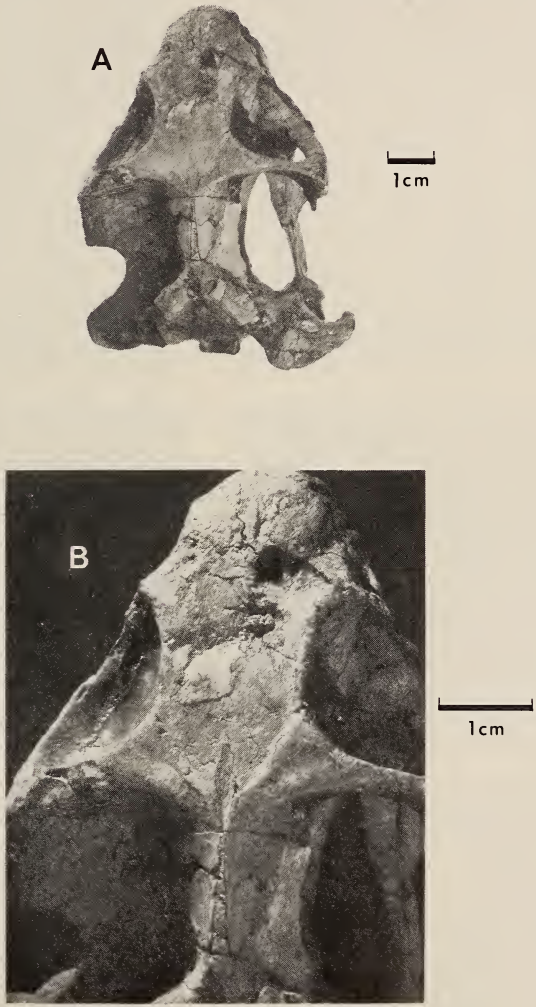

PLATE 1. *Kombuisia frerensis*. No. 430.

A. Skull, dorsal aspect. B. Parietal region, enlarged to show condition of bone surface and absence of pineal opening.

sided as in most dicynodonts, but tapers forward to a squared-off anterior margin. Median groove between dentary tables, which is deep and distinct in nearly all dicynodonts (Crompton & Hotton 1967), is very shallow in *Kombuisia*; in fact, dentary tables are separated from median groove only by a pair of low, sharp ridges that run straight back from the corners of the squared-off anterior margin of the beak. Lateral and parallel to each of these ridges is a low, rounded ridge

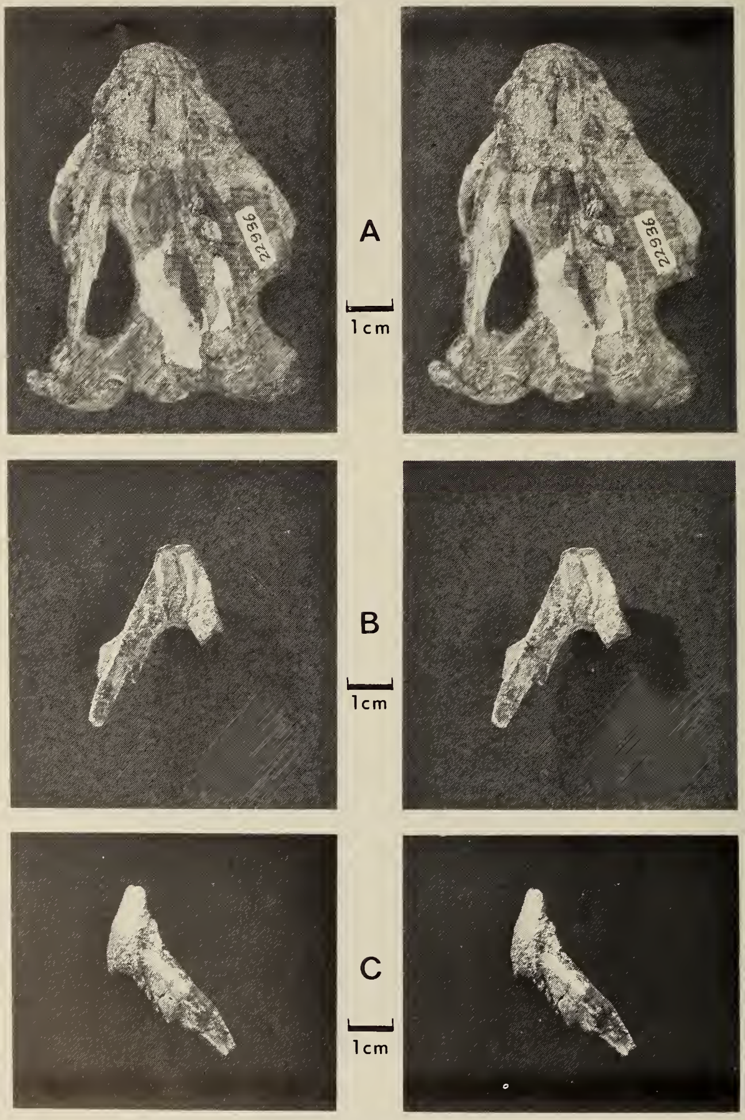

Plate 2. *Kombuisia frerensis*. No. 430. Stereo pairs.
A. Skull, palatal aspect. B. Dentary, dorsal aspect. C. Dentary, left lateral aspect.

that rises at the symphyseal margin about half-way between the tip of the beak and the splenial margin, and runs back to disappear a little behind the splenial margin.

Discussion

The most distinctive single feature of the type of *Kombuisia* is that it has no pineal opening. In the type specimen, the pineal region of the skull roof is virtually undistorted and the surface of the bone is undamaged (Plate 1 B); there is thus no evidence of pathology and the lack of a pineal opening appears to be the normal condition. A second specimen (National Museum, Bloemfontein, C. 3006, excellent stereophotographs of which were provided by A. R. I. Cruickshank) comes from a *Cynognathus* zone locality and is clearly referable to *Kombuisia* on the basis of palate and dentary symphysis. Unfortunately the Bloemfontein specimen consists of snout and dentaries only, and the presence or absence of a pineal opening cannot be confirmed. Because the lack of a pineal opening is so unexpected in dicynodonts, and because at present it is indicated in *Kombuisia* by only the one specimen, I prefer to delay incorporating this character into the formal diagnosis of the genus until more evidence comes to light.

The two identified specimens of *Kombuisia* are very nearly the same size, and are slightly less than half as large as the genotype of *Kingoria*, University of Tübingen, catalogue number K. 12. This specimen, as well as those described by Cox, appear to have been adult at the time of death, as does the type of *K. galecephalus* (Broom & Robinson 1948), Rubidge Collection, catalogue number 97.[4] The type of *Kombuisia*, though smaller, does not appear to have been appreciably younger at time of death than the various specimens of *Kingoria*, and it is therefore probably close to the adult size of the genus.

Kombuisia and *Kingoria* are most usefully compared with the more common Beaufort dicynodonts, animals of small to moderate size that lack postcanine teeth, including *Dicynodon* as it is generally accepted at the present time, and *Lystrosaurus*. The genus *Dicynodon* is under study by the writer and M. A. Cluver, and there is every indication that the name as currently used includes two distinct genera. However, differences between these groups are not critical to comparison with *Kombuisia* and *Kingoria*, and for present purposes the name *Dicynodon* is employed in its current usage. The informal term 'common dicynodonts' as used in the remainder of this discussion includes both *Dicynodon*, in this inclusive sense, and *Lystrosaurus*.

Neither the type nor the Bloemfontein specimen of *Kombuisia* has any trace of tusks. The caniniform processes are small and the snout is short and delicate. These facts alone are not sufficient to indicate that tusks were absent in all

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[4] Listed by Haughton & Brink (1954) as catalogue number 77 (*in errore*). Number 77 is the type of *Dicynodon clarencei* Broom, which Haughton & Brink list incorrectly as number 97. The two specimens are quite distinctive, and the error seems to be simply a matter of catalogue numbers having been switched inadvertently.

individuals of the genus for, as Broom notes (1935), tuskless specimens of *Dicynodon grimbeeki* have more lightly-built snouts than tusked specimens. Cox reports that only two of ten specimens of *Kingoria* at his disposal had tusks, but describes no differences between the snouts of tusked and tuskless individuals. However, in *Kombuisia* the snout is more delicate and the caniniform processes are proportionately smaller than in most other dicynodonts, including tuskless specimens of *Kingoria* and *D. grimbeeki*, and it seems unlikely that any individuals of *Kombuisia* had tusks.

The palates of *Kombuisia* and *Kingoria* are distinctive in their lack of relief. In most dicynodonts (cf. Ewer 1961; Crompton & Hotton 1967; Cluver 1970, 1971) there is a pair of strong ridges on the back of the premaxillary beak, one on either side of the midline, and the contact between the vomer and the premaxilla is produced into a prominent midline ridge. In *Kombuisia* and *Kingoria* the premaxillary ridges are lacking and the midline vomerine ridge is much subdued; there is, however, a low, longitudinal ridge just medial to each maxillo-premaxillary suture (Fig. 1: LR) which is not present in other dicynodonts.

The punctate and rugose sculpture on the beaks of dicynodonts is generally agreed to indicate the presence, in life, of a horny covering, because of its resemblance to comparable areas in birds and chelonians. On the rostral

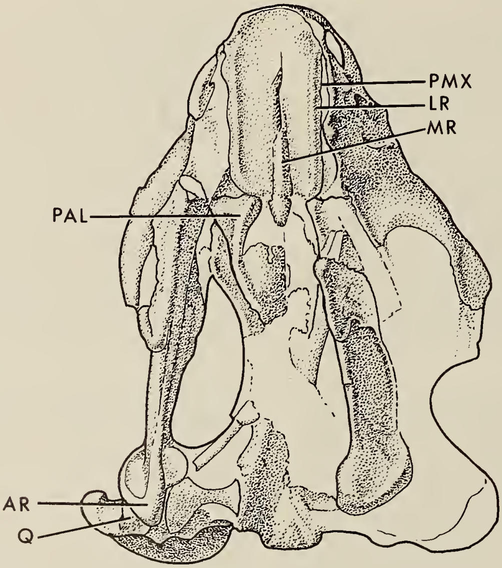

Fig. 1. *Kombuisia frerensis*. No. 430.

Skull, palatal aspect: AR, articular; LR, longitudinal ridge at lateral edge of premaxilla; MR, median ridge at junction of premaxilla and vomer; PAL, palatine; PMX, maxillo-premaxillary suture; Q, quadrate.

surface of the snout and on the dentary symphysis the distribution of this covering must have been relatively uniform throughout the Dicynodontia; it is much the same in *Kombuisia* and *Kingoria* as in other dicynodonts. On the buccal surfaces of the palate, however, it shows much greater variation; *Kombuisia* and *Kingoria* represent one extreme and common dicynodonts the other, and these extremes parallel the differences in relief of the palate. In common dicynodonts the entire buccal surface of the palate is punctate, even to the hollows between the ridges, and was presumably entirely covered by horn. In *Kombuisia* and *Kingoria*, punctate sculpture, and hence a putative horn covering, is restricted to the buccal surfaces of premaxilla and maxillae, to the latero-posterior corners of the premaxilla, and to the small palatal processes of the palatines adjacent to the latter. This leaves most of the premaxillary secondary palate smooth and presumably covered by mucous membrane, much like the mesial surface of the palate in chelonians. Because punctate sculpture is not developed medial to the low, longitudinal ridges at the lateral margins of the premaxilla in *Kingoria*, Cox (1959) suggests that these ridges merely reflect the medial margins of horn covering. The structure of *Kombuisia* should probably be interpreted in the same way.

In the common dicynodonts, the horn-covered secondary palate, with its elaborate system of ridges and rugosities, is associated with a mouth of trenchant appearance: maxillary and premaxillary margins are blade-like, the dorsolateral margins of the dentary symphysis are squared off, and the tip of the dentary beak supports a transversely oriented blade. This arrangement forms a system of blades and surfaces on the upper and lower jaws (Crompton & Hotton 1967) that comminuted food by a shearing action, the force being provided by retraction of the jaw; it probably arose co-ordinately with the retractive sliding action of the jaw that defines the Dicynodontia as a group. In various pristerodonts and *Lystrosaurus* (Crompton & Hotton, 1967), and in most other dicynodonts as well, the jaw joint is characteristically very unstable in full protraction, because the bearing surfaces of the joint that are in contact during full protraction, i.e. the posterior surface of the articular and the front of the quadrate, are both convex. Because of this instability, the vertical force that could be exerted on the jaw at this time was limited to the small vertical component of the very obliquely directed anterior fibres of the temporalis musculature, which served primarily to initiate elevation of the jaw. Elevation and retraction were concurrent, but the bulk of force exerted on the lower jaw in early stages was horizontal, and the motion that was most effective in shearing was retraction. The more vertically oriented posterior temporalis fibres must have been relaxed at protraction, and came fully into play only as the jaw approached full retraction.

In *Kombuisia* and *Kingoria*, in which the secondary palate lacks horn covering and marked relief, the appearance of the mouth is less trenchant than in most other dicynodonts. Although maxillary and premaxillary margins are sharp in *Kombuisia*, the shallow palate is occluded by a flattened, spatulate dentary. The lateral premaxillary ridges are not comparable in either position or prominence to the ridges of common dicynodonts. In *Kingoria*, both upper and lower jaw margins appear to be rounded and smooth, and the tip of the beak tapers to a blunt point. The palate is deeper than that of *Kombuisia* but is equally featureless.

Reduction of trenchancy of mouth and palate suggests marked modification of the shearing function in *Kombuisia* and *Kingoria*. In *Kingoria* this modification does not seem to have affected the jaw mechanism, which is much the same as in other dicynodonts, but in *Kombuisia* it apparently extends to the jaw joint. The lower jaw of the type specimen of *Kombuisia* is articulated in full protraction, and the right articuloquadrate joint is quite well preserved and exposed. The retroarticular portion of the articular bone is produced backward so that the lower (and posterior) part of the bearing surface lies beneath the quadrate in full protraction (Fig. 1 : AR), rather than in front of it as in most dicynodonts. The posterior bearing surface is therefore somewhat concave, so that the surfaces of quadrate and articular are more nearly congruent and the joint is correspondingly more stable when the jaw is fully protracted. Thus it is possible that in *Kombuisia* greater vertical force could be applied at the beak much earlier in the cycle, perhaps even during full protraction.

The mouth of *Kombuisia* more than that of any other dicynodont is like the mouth of many chelonians, in the characteristic flatness of the dorsum of the dentary symphysis and the restriction of horn to the margins of the palate. Furthermore, the ridges at the lateral margins of the premaxilla (Fig. 1 : LR) appear to meet the dentary tables, i.e. the grooves between each of the pairs of lateral ridges on the dorsum of the dentary (Plate 2 B), when the jaw is at or close to full protraction. The dorsum of the symphysis thus appears to be more nearly congruent to the buccal surface of the shallow palate than in most dicynodonts, another characteristic reminiscent of chelonians. There is no doubt that *Kombuisia* retained the retractive sliding mechanisms of the dicynodont jaw, but the stability of the joint during protraction, coupled with morphological features of the mouth, suggest that it had superimposed a more turtle-like anterior bite upon the basic dicynodont jaw mechanism.

Conclusions about the habits of *Kombuisia* must await the appearance of new material, for verification of the patterns described here and for information as to the postcranial structure of the animal. The possibly superficial resemblance of the feeding mechanism to that of chelonians is not very useful in this context, for chelonians exhibit the widest range of habitats and habits of living reptiles. However, the fact that the clearest distinctions among *Kombuisia*, *Kingoria* and most other dicynodonts are associated with the feeding mechanism indicates that dicynodont radiation, like dicynodont origin, was primarily a matter of exploiting the possibilities of different modes of feeding.

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